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ENTOMOLOGY.—*Phylogeny and biogeography of the caddisflies of the genera Agapetus and Electragapetus (Trichoptera: Rhyacophilidae)*.<sup>1</sup> HERBERT H. ROSS, Illinois Natural History Survey, Urbana, Ill.

An analysis of the phylogeny and distribution pattern of the small caddisflies belonging to the genus *Agapetus* and its allies has presented some interesting data on the movement of faunal elements between North America and Eurasia. For insects the time relations of this entire phase of distribution is poorly understood, although there is evidence in most groups of crossings between the parts of Holarctica. In the *Agapetus* group there is some evidence for placing such crossings in relation to geologic time.

The results of this study of the *Agapetus* line attest the fact that many small insect genera occupy a unique place in unraveling the phylogeny and morphogenetic steps in a large number of groups. This has been stressed by Emerson (1950) in his remarks on the objectivity of monotypic genera. In many instances these small genera are surviving members of early points in phyletic lines that have developed abundant faunas specialized far beyond these relicts. We are justified in regarding such archaic survivors as living fossils. In insect studies they are what we must use as a basis for phylogenetic deduction in theoretical areas of evolutionary speculation. In groups such as vertebrates and Mollusca, fossil evidence is used in this capacity.

It is my conviction that, by and large, insect groups possess more living fossils than vertebrate groups do true fossils and that, as a consequence, the entomologist has an unusual opportunity to contribute material

basic to the study of biogeography and evolution.

*Electragapetus* is one of those archaic genera of which, fortunately, we have available both a well-preserved fossil and two existing species. Its study establishes the order of origin of the distinctive characters of *Agapetus* and allows the dating of at least part of the associated phylogenetic development. With this as a basis a preliminary analysis has been attempted of the origin, divergence, and dispersal of the entire *Agapetus* complex.

#### THE AGAPETUS LINE

The genus *Agapetus* represents a phyletic line (Fig. 15) that arose from the genus *Anagapetus* and that is characterized in the adult primarily by a reduction and reorganization of the veins of the hind wing. The apex of development in these characters occurs in the *fuscipes* complex of the genus *Agapetus*.

In *Anagapetus* the front wing (Fig. 1) is much like *Rhyacophila*. The hind wing is also little changed from the primitive rhyacophilid type; its radial field (Fig. 6) has all branches present and the forks of  $R_s$  occur before cross-vein  $s$ ; and the anal veins are all present, with 1A and 2A forming an elongate fork. The genus *Catagapetus* represents the first steps toward *Agapetus*. In *Catagapetus* the front wing has lost vein  $R_{1+2}$ , and cross-vein  $r$  has become aligned with cross-vein  $s$  (as in Fig. 2); and in the hind wing (Fig. 7) cross-vein  $s$  has moved basad. Existing species show reductions of hind wing venation that have occurred in the *Catagapetus* line since it separated from the main *Agapetus* stem.

In *Electragapetus* (Fig. 8) the first major steps in specialization are seen: fork  $R_{2+3}$  has migrated

<sup>1</sup>This paper is a joint contribution from the Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey, and the Department of Entomology, University of Illinois.

close to the margin of the wing, fork  $R_{4+5}$  has migrated a short distance in the same direction, and cross-vein  $s$  has migrated closer to the basal fork of  $R_6$ . The more primitive existing species of *Agapetus*, such as the species *dubitans*, exhibit a marked change in this hind wing pattern (Fig. 9). Beyond cross-vein  $r$ ,  $R_1$  is reduced to a short, oblique section fusing with  $Sc$ ; the basal part of  $R_1$ ,  $r$ , and  $R_{2+3}$  beyond  $r$ , have realigned to form a serial vein with a slight dip on the part of the vein composed of  $r$ ; cross-vein  $s$  has completely disappeared; and  $R_{4+5}$  branches much closer to the wing margin. This early point in *Agapetus* development is called the *Synagapetus* stage, and its origin is labeled S.S. in Fig. 15.

Between the *Electragapetus* stage and the *Agapetus* stage of evolution of the radial veins, a second development of the hind wing venation took place. In *Anagapetus* and *Electragapetus* (Fig. 6) vein 3A is short and free, running into the margin of the wing. In *Agapetus* (Fig. 9) it appears to have turned up at the end and run into vein 2A just beyond cross-vein  $a$ . The short stub projecting from the curved connection, however, may actually be the tip of 3A and the connecting portion may be an adventitious spur or branch that has developed as a cross brace. Following this interpretation, when the stub is present it is labeled 3A and the connecting piece 3A'; when the stub is absent the vein is labeled simply 3A.

After the change began in the anal veins, reduction still continued in the anterior veins, involving first a complete loss of the oblique section of  $R_1$  running from  $r$  to  $Sc$ , and then both a coalescence of  $Sc$  with the anterior margin, and continued movement of the forks of  $R_6$  toward the wing margin. The end of this direct line is represented by the European *fuscipes* (Fig. 13) in which all but the base of  $Sc$  has coalesced with the anterior margin, fork  $R_{2+3}$  has become completely obliterated, and fork  $R_{4+5}$  is very close to the wing margin. Throughout this series little change occurs in the front wing or in the anal region of the hind wing. This sequence of reduction of venation has proceeded independently in several distinct phyletic lines within *Agapetus*, and reached various stages in different lines.

A somewhat similar situation exists regarding the male genitalia in the *Agapetus* complex. From at least the origin of *Electragapetus*, the ancestral form of genitalia has had single segmented clasp-

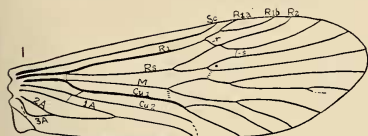
ers, the tenth tergite divided into a pair of vertical, platelike, and only partially sclerotized lobes, and at the base of each lobe a fingerlike, projecting cercus bearing an irregular row of long setae (Fig. 23A). Differences in genitalia between most of the species involve chiefly differences of proportion or addition of ornamentation to this general basic type. That is, in one species the tenth tergite may be long, in another species short; or in one species the clasper may have a mesal spur, in another none. In certain lines, however, there is a marked reduction of the cercus, and in a few lines this structure has completely disappeared. Judged from evidence from other structures, the same modifications have arisen independently in different lines.

#### PHYLETIC BRANCHES OF AGAPETUS

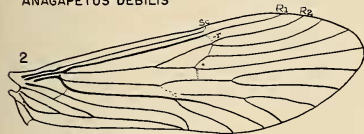
Evidence indicating the first major division of *Agapetus* is found in a curious pair of organs occurring one on each lateral portion of the fifth sternite of the males. In some species this organ is internal and forms an oval or round cavity opening by a narrow slit to the outside. Its function is probably olfactory or auditory. Beginnings of this organ are found in some of the primitive species placed in the subgenus *Synagapetus*, such as *dubitans* and especially *iridipennis*, in which an invagination is present beneath a ridge on the side of the fifth sternite. The organ is present as a well-developed structure in many of the European species and all the American species, but absent in all the Japanese and East Pacific Island species I have seen.

This latter group of Oriental species thus appears to be an independent evolutionary line, starting from a primitive species of *Synagapetus* representing a stage before the lateral male organ had begun to develop. The genitalia have remained primitive in essential respects throughout the line, but the hind wing venation has become progressively reduced to the condition found in *curvidens* (Fig. 14) in which not only radius but also the branches of media are greatly reduced. This complex of species I am calling the *curvidens* line.

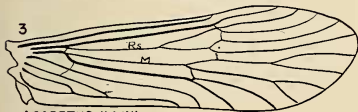
The other species in *Agapetus* form a line also stemming from a primitive *Synagapetus* type, but a line which branched into several subsidiary developments. One of them culminated in the *membrosus* complex, another in the relatively primitive *comatus* complex, a third in the *fuscipes*



1  
ANAGAPETUS DEBILIS



2  
ELECTRAGAPETUS TSUDAI



3  
AGAPETUS ILLINI



4  
AG. MEMBRUSUS



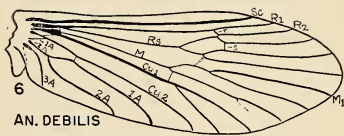
5  
AG. CURVIDENS

FIGS. 1-5.—Front wings of the *Agapetus* line.

complex, these three apparently confined entirely to Eurasia, and a fourth which gave rise to the American species of *Agapetus*.

There are other lines that I am unable to place phylogenetically in satisfactory fashion but that probably originated as close relatives of the *comatus* group. These include the following, tentatively considered as subgenera of *Agapetus* until detailed study allows more exact treatment: *Myspotele* Barnard, from South Africa; *Afragapetus* Mosely, from the mountains of east-central Africa; *Allagapetus* Martynov, from Turkestan and India; and *Lanagapetus* Mosely, from Madeira.

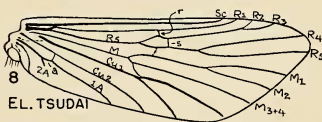
The American species exhibit two circumstances suggesting their position in relation to the Eurasian fauna. In the first place, although



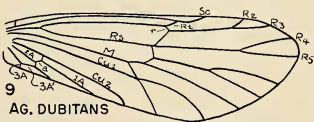
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AN. DEBILIS



7  
CAT.  
NIGRANS



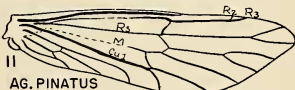
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EL. TSUDAI



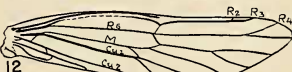
9  
AG. DUBITANS



10  
AG. ILLINI



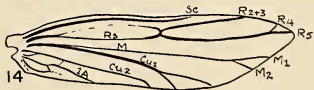
11  
AG. PINATUS



12  
AG. MEMBRUSUS



13  
AG. FUSCIPES



14  
AG. CURVIDENS

FIGS. 6-14.—Hind wings of the *Agapetus* line: Ag., *Agapetus*; An., *Anagapetus*; Cat., *Catagapetus*; El., *Electragapetus*. (Fig. 7 after McLachlan; Fig. 9 after Mosely.)

the American fauna contains many diverse types of genitalia, they appear to be related to each other rather than to various known complexes of the Eurasian fauna. In the second place, the base of the various lines begins with forms having a relatively primitive hind wing venation (Fig. 10) little changed from the primitive *Synagapetus* wing (Fig. 9). This indicates that the American fauna probably arose from a single ancestor which crossed from Eurasia to North America, and that this ancestor was a primitive form of the *Agapetus* branch which developed the lateral male organ. None of the American species have undergone a great deal of evolution as regards venation. The primitive species such as *boulde-rensis* and *illini* have in the hind wing a faint trace of the base of  $R_1$  (Fig. 10) and definite angulations where  $r$  joins  $R_1$  and  $R_{2+3}$  and in the males a fairly long cell  $R_2$ . The most specialized wings differ only in that the serial radial vein has become smoother in the region of  $r$ , all trace of  $R_1$  beyond this point is lost, and cell  $R_2$  is short in both sexes (Fig. 11).

The relationships of the genera and the known lines of *Agapetus* are shown in Fig. 15. This chart shows the few specialized lines of *Agapetus* actually studied, and in addition an approximation of the origin of the African lines. While the nature of the lateral male organ is not known for the African species, the venation and male genitalia are relatively generalized and indicate that these arose from a form essentially like that persisting in the *comatus* line.

BIOGEOGRAPHY

With the exception of the Baltic amber *Electragapetus scitulus*, the data for biogeographical analysis of the group under discussion consist entirely of the known distribution patterns of existing species. These patterns are fragmentary for many species, but nonetheless they bring out certain points that should furnish at least a starting point for needed further study in this field.

Judged from the habitat or climatic preference of all existing species, the group is and always has been restricted to clear, cold, small streams or brooks. The only exception is the subgenus *Tagapetus*, which probably inhabits warmer streams than is typical for other species. This cold-adapted characteristic of the group means that all spreading of range occurred only through territory where such streams were relatively

numerous. For range extensions from Eurasia into Africa, a mountain highway would have been imperative in order to afford these stream conditions through the equatorial belt.

The ancestral genus *Anagapetus* is quite successful in many montane localities in North America in competition with both *Glossosoma* and *Agapetus*. From this it would seem probable that if it had ever occurred in Eurasia, some remnant of it would still survive and have been found. On the same grounds of competitive behavior, the genera *Catagapetus* and *Electragapetus* may be ascribed to an existence confined to Eurasia. Since this constitutes our only evidence, I am following it as a general precept.

DISPERSAL AND EVOLUTIONARY LINES

The *Catagapetus*-*Agapetus* line (Fig. 15) probably started in late Cretaceous or early Cenozoic time as a population of *Anagapetus* which spread

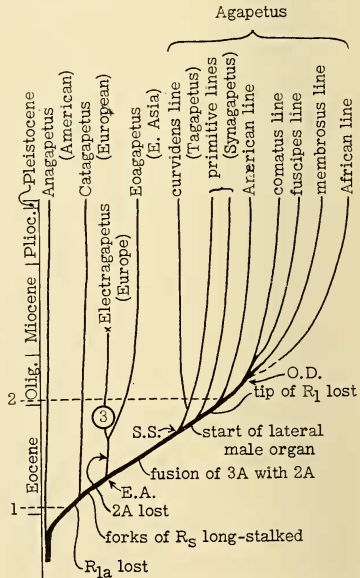


FIG. 15.—Diagram of phylogeny of the *Agapetus* line: E.A., *Electragapetus* ancestor; S.S., *Synagapetus* stage; A.A., *Agapetus* ancestor. 1, early Eocene dispersal; 2, early Oligocene dispersal; 3, approximate horizon of fossil *Electragapetus*.

from North America into Eurasia. This gave rise first to a *Catagapetus*-like form differing in only a few morphological respects from its progenitor. From this form arose a more modified form, in which the hind wing underwent reduction of venation and produced a form much like *Electragapetus*, but retaining all of vein 2A in the hind wing. This, the *Electragapetus* Ancestor, must have become widespread, divided, and had its parts isolated geographically, for it gave rise to two distinct phyletic lines, leading to *Electragapetus* and *Agapetus*, respectively.

The *Electragapetus* line remained very like its ancestor, changing only slightly in venation. It had developed into a definitive *Electragapetus* morphotype by late Eocene or early Oligocene, and it is a matter of record in the Baltic amber that it occurred at this time in the vicinity of Germany. Eventually its range embraced all Eurasia, as witnessed by living species in eastern Siberia and Japan.

The *Agapetus* line underwent continued reduction in hind wing venation, and reached the *Synagapetus* stage before a successful, long range, competitive form was evolved. This type also became widespread over Eurasia, with existing species having primitive types of genitalia surviving in China, India, and many areas in Europe, and more specialized species in Japan and Madeira. There is one record, based on a female specimen, from northern Ontario, Canada, which may indicate a spread of the group through northern North America, but pending knowledge of the male no interpretation of this record will be attempted.

This primitive *Synagapetus* group gave rise to a line that may have become isolated in the islands to the east of the Asiatic coast. Its only known members are now recorded only from Japan, the Philippine Islands, Java, and New Guinea. The line has undergone much change, culminating in the *curvidens* complex.

Other *Synagapetus* stock developed a curious lateral organ on the fifth sternite of the male. After this development there occurred a spread of the line throughout continental Eurasia and into North America and possibly also Africa. Each of these extensions of range is represented today by an isolated and frequently highly distinctive group. From this it seems certain that after the range extension occurred, most of the avenues of dispersal became ecologically unsuitable for *Agapetus* and have remained so since.



FIG. 16.—The dispersal cycle of the *Anagapetus* to *Agapetus* evolutionary line. In the upper map the present distribution pattern of the generalized species of *Agapetus* (chiefly *Synagapetus*) is diagrammed as the sinuate oval across Eurasia.

Otherwise we would expect a mingling of diverse faunal units in the periphery of the range of the group. It is likely that this radiation was made possible by the extensive orogenies culminating in the Miocene, which provided avenues of dispersal across the old sea Tethys and gave rise to the African mountains and many of the extensive ranges in southern Europe and Asia.

The retention of the stub of  $R_1$  in the hind wing of primitive American species indicates that this line resulted from a population which spread into North America before the European and African progenitors had evolved. The monophyletic nature of the existing American fauna indicates that no later dispersals occurred from Asia, and the Asiatic fauna indicates that no American forms spread back to Asia.

#### TIME RELATIONSHIPS

The problem of fixing the evolutionary sequence in Fig. 15 calls for a matching of known or inferred time of events based on information from the *Agapetus* data with possible dispersal opportunities deduced from studies of other

groups. In this latter connection I have drawn chiefly on the summary of Holartic mammal dispersal given by Simpson (1947).

The Oligocene Baltic amber fossil *Electragapetus* provides us with one approach to the dating problem. Referring to Fig. 15, we see that—

1. There must have existed an ancestor common to both *Electragapetus* and *Agapetus*, which possessed a hind wing like Fig. 8 but which retained vein 2A, still preserved in *Agapetus*. This ancestor is indicated as E. A. in Fig. 15.

2. The *Electragapetus* line lost 2A. The time which elapsed during this loss represents the time interval between E. A. and the formation of the generic characteristics of *Electragapetus* as it appears in Oligocene amber and today. There is no evidence to indicate how far this occurred up the *Electragapetus* line, so in Fig. 15 this must first be placed arbitrarily as an indeterminate period. It is highly likely that the *Electragapetus* line continued as a viable, primitive line for some time after the separation of *Eoagapetus*. The assumed point of extinction of the *Electragapetus* line is terminated by an "x." This point is purely arbitrary.

3. In the fossil *Electragapetus* hind wing, vein 2A is atrophied to cross-vein *a*. In subgenus *Eoagapetus* there is still a vestige of this vein. On this evidence, the division between the two occurred before early Oligocene from which the fossil is known. This places the time of E. A. as definitely pre-Oligocene and further places the time of the spread of *Anagapetus* into Eurasia as considerably before Oligocene.

Another suggested dating occurs at point O. D. (Old World dispersal of *Agapetus*). Shortly after the spread of *Agapetus* to North America (morphologically speaking) there occurred a dispersal of *Agapetus* to the various mountainous regions of southern Eurasia and Africa. Since Africa is involved, this spread could hardly have occurred prior to the shrinkage of Tethys in the Miocene; it is also likely that suitable mountain habitats were not available in Africa and parts of southern Eurasia until the orogenies producing the shrinkage of Tethys had progressed to an advanced stage. It is also apparent that following the spread of a primitive *Agapetus* there was an isolation of populations in various areas, an isolation that has persisted to the present. During this period each isolate has developed into a distinctive taxonomic entity.

Turning to evidence that Simpson (1947) has assembled from distribution of mammalian fossils, there is found a remarkably close correlation with certain conclusions. Simpson postulates that (1) there was a relatively complete interchange of American and Eurasian forms in early Eocene, (2) a lesser but extensive interchange in early Oligocene, and (3) small interchanges of only limited ecological types until late Pliocene. Although Pliocene and Pleistocene interchanges were not made by *Agapetus*, the first two points fit very well with the analysis made of the genus.

Evidence from the phylogeny of the Rhyacophilidae (Ross, 1951) gives every reason to believe that *Anagapetus* had evolved by middle or late Cretaceous. It could have spread into Eurasia on an early Eocene bridge, and the Eurasian isolate start on the evolutionary road to *Agapetus*. If this time of crossing is correct, the Eurasian line evolved fairly rapidly through ancestral *Catagapetus* and *Electragapetus* stages and past the early *Agapetus* stage (that is, *Synagapetus*) before Oligocene. Presumably the specialized *Agapetus* line had just begun to evolve when a species of its early complex spread into North America and then was cut off on this continent. The slightly more specialized European continuation of the line spread in Miocene to its present outposts.

This explanation satisfies the conditions that E. A. be pre-Oligocene, and that O. D. be late Oligocene or Miocene. Beyond these limits, of course, the branchings in Fig. 15 are simply "reasonable estimates."

One question arising from this explanation is of more than usual interest. When *Agapetus* spread into North America, why did not *Catagapetus* and/or *Electragapetus* spread with it? They were both extant somewhere in Eurasia at that time. It is quite possible that they may yet be found in North America, for many mountain regions of the Northwest are virtually uncollected; or they may have made an entry and the colony become extinct. It is also possible that these two genera were confined to Europe or Western Asia during early Oligocene. A third and highly plausible alternative is that *Agapetus* had developed an ecological tolerance for warmer streams than the other two, and that in the Oligocene conditions on the Bering bridge were opportune for *Agapetus* but not for the others.

## TAXONOMIC NOTES

Certain of the deductions made in the preceding pages are based on new species, which are described below. Unless otherwise stated, types are in the collection of the Illinois Natural History Survey.

Genus *Electragapetus* Ulmer

This genus was described to include a single fossil species, *scitulus* Ulmer, from Baltic amber. Later Martynov described the genus *Eoagapetus* to receive a living species, *praeteritus* Martynov, from eastern Siberia. The venation of the two is virtually identical, the differences between the two groups being mainly in male genitalia. This relationship seems best expressed by considering the two groups as subgenera, as follows:

*Cercus* digitate, projecting free from narrow base, similar to condition shown in Fig. 21A

*Electragapetus*

*Cercus* low, with basal attached portion very long, apical edge with a row of fine setae, Fig. 17A

*Eoagapetus*Subgenus *Eoagapetus* Martynov

## KEY TO SPECIES

- Lobes of tenth tergite symmetrical, each with a short lateral point at tip; cercus evenly crescent shaped; clasper with apical margin notched to produce a wide dorsal and very narrow ventral lobe. . . . . *praeteritus* Martynov
- Lobes of tenth tergite asymmetrical, right lobe inconspicuous and membranous, left lobe sclerotized and with its ventral angle produced into a long slender finger; cercus with ventral portion larger than dorsal; clasper simple, Fig. 17. . . . . *tsudai*, n. sp.

*Electragapetus tsudai*, n. sp.

Many characters of the genitalia differentiate this species from *praeteritus*, summarized in the preceding couplet.

*Male*.—Length 8 mm. Color dark brown, legs and venter slightly lighter than dorsal portion. General structure, including wing venation, Figs. 2 and 8, typical for genus. Fifth abdominal sternite with only slightly embossed lateral areas. Genitalia as in Fig. 17. Tenth tergite with right lobe membranous and inconspicuous, left lobe with ventral corner digitate and long, angled both ventrad and laterad. Cercus forming a short but very deep flap, extending ventrad over the base of the clasper. Clasper with lateral aspect regular, rounded at apex, and nearly twice as

long as deep; both upper and lower margins have a sclerotized tooth a third distance from apex. Aedeagus very long, with a pair of long sclerotized rods, one flattened and convoluted before the spinelike apex, the other slender, more rounded, and nearly straight.

*Holotype*.—Male; Higashiyama, Fukushima Pref., Japan, May 24, 1949, Mrs. M. Kohno.

*Paratype*.—Yu River, Higashiyama, Kita-aizugun, Fukushima Pref., May 24, 1949, Mrs. M. Kohno.

Genus *Agapetus* Leach

Arriving at a workable classification for this genus has been difficult. While the species resolve into separate phyletic lines, the primitive members of a line sometimes differ little from members of unspecialized lines, but the end species of the line may be radically different from any other species in the genus. It is desirable to make special subgeneric categories for the very unusual forms, yet it seems impractical to make a separate subgenus for every phyletic line.

Subgenus *Synagapetus* McLachlan

To this subgenus authors have usually referred species in which hind wing  $R_1$  joins Sc, Fig. 9, and the female middle tibiae are dilated. It is now apparent that this simple definition is in need of revision, but a more thorough understanding of the genus is required to reach a satisfactory result. For purposes of the present I am considering *Synagapetus* as a broad unit, including species previously placed in *Synagapetus* and *Pseudagapetus*, and a third group having hind wing  $R_1$  lost at its tip but with no male lateral organ. This latter group includes *japonicus* Tsuda, and three New Guinea species described here. At the evolutionary apex of the line stand the Philippine species *curvidens* Ulmer (Fig. 14) and the Java species *abbreviatus* Ulmer. These two are so distinct from other members of their line that they have evidently come under the influence of new, strong selection pressures and started a divergent branch of their own. A new subgenus is therefore erected for their reception.

*Agapetus ulmeri*, n. sp.

The very simple male genitalia and venation indicate this as one of the primitive members of the genus. The angulate anterior margin of the ninth segment, however, in this and the two

following species indicates that they are offshoots from the base of the *curvidens* line. The short, truncate tenth tergite lobes combined with the slender clasper differentiate this species from its relatives.

*Male*.—Length 3.5 mm. Color dark brown, the legs and venter slightly lighter. General structure typical for genus, venation similar to that of *illini* female, but the hind wing with no vestige of the tip of  $R_1$  and with no pronounced dip in the  $R_1$  serial vein at  $r$ . Front tibia with inner apical spur much shorter than outer, both fairly small. Fifth abdominal sternite with simple embossed area. Genitalia as in Fig. 19. Ninth segment with anterior margin broadly but fairly sharply angulate. Lobes of tenth tergite deep and short, truncate at apex, and each with a dorso-lateral flange above cercus. Cercus finger-like, with four long setae. Clasper simple, the apical portion narrowed, straight, and without sclerotized points. Aedeagus with simple rods sharply upcurved at apex.

*Holotype*.—Male; Hollandia, New Guinea, rain forest, March 22, 1945, H. Hoogstraal.

#### *Agapetus jafiwi*, n. sp.

This species is most closely related to the preceding, from which it differs in the shape of the tenth tergite lobes and the produced anterior margin of the ninth segment.

*Male*.—Length 4 mm. Color and general structure, including wing venation and fifth abdominal segment, as in the preceding species. Genitalia as in Fig. 20. Ninth segment fairly long both dorsad and ventrad, its anterior margin produced into a long internal projection with a pointed apex. Tenth tergite with each lobe fairly long and deep, with a recurved, small, dorsal hook and the extreme apex also forming a hook-like projection. Cercus short and stout, with four long setae. Clasper long, with base only moderately wide, apex pointed, and with a pointed ventromesal flap just before the apex.

*Holotype*.—Male; Hollandia, New Guinea, March 15, 1945, at light, near Jafiwi, H. Hoogstraal.

#### *Agapetus latosus*, n. sp.

The tenth tergite lobes in this species have a most curious shelllike lateral overhang which is unlike anything else illustrated in the genus. Other characters, especially the produced ninth

segment and simple clasper, indicate that this is another member of the *curvidens* line.

*Male*.—Length 3.5 mm. Color, general structure, venation, and characters of the fifth abdominal sternites as for the preceding species. Genitalia as in Fig. 22. Ninth segment narrow dorsad, longer than usual ventrad, the anterior margin produced into a large, trianguloid, rounded projection. Tenth tergite lobes deep at base, with a lateral, irregularly serrate overhang; the apex of each lobe forms a triangular, slightly downcurved piece the base of which fits under the lateral overhang. Cercus elongate and slender, with four setae on apical third, its dorsal aspect appearing a little bulbous at base. Clasper with lateral aspect short, parallel sided and rounded at apex; ventral aspect with a mesal point at apex, and with basal half wide. Aedeagus with simple rods.

*Holotype*.—Male; Doromena, Netherlands New Guinea, February 25, 1945, Hoogstraal and Jewett.

*Paratypes*.—Same data, 2 ♂.

#### *Tagapetus*, n. subg.

*Characteristics*.—General structure of head and body typical for genus. Diagnostic differences in venation are as follows: front wing (Fig. 5) with fork  $R_{4+5}$  very narrow, and cross-vein  $s$  long, so that vein  $R_4$  is much closer to  $R_5$  than to  $R_3$ , and with both forks of  $M$  close to margin of wing; hind wing (Fig. 14) with  $Sc$  distinct from margin, the two principal radial veins very close together at center of wing, and vein  $M_{3+4}$  and cross-vein  $m-cu$  entirely atrophied; in addition the hind wing has  $R_{2+3}$  unbranched,  $R_{4+5}$  with a very short branch, and apex of  $2A$  reduced to an indistinct stub.

*Genotype*.—*Agapetus curvidens* Ulmer.

In addition to the genotype, *Tagapetus* includes *abbreviatus* Ulmer from Java.

The male genitalia of the genotype (Fig. 21) exhibit many characteristics of the generalized type, with the addition of the slender, elongate and sinuate clasper and the anterior sharp projection of the ninth segment. These characters of genitalia leave no doubt but that *curvidens* is one of the end products of its phyletic line. The unusually great differences in wing venation also indicate clearly that the two species in the subgenus have undergone very rapid evolution compared to all other members of their line.

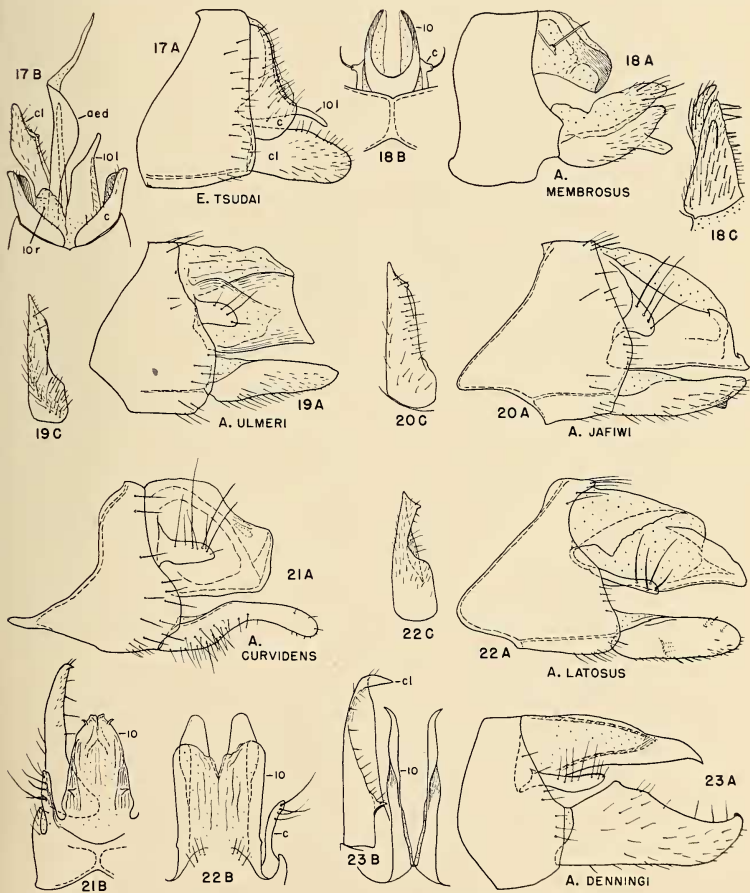


Subgenus *Agapetus* Leach

The subgenus *Agapetus* is defined here as the general group in which the tip of  $R_1$  is atrophied in the hind wing, and the lateral abdominal organ of the male is well developed as a round or ovoid internal structure.

*Agapetus membrus*, n. sp.

This species is one of the end branches of the *membrus* line, differing from the *bidens* group in having the apex of both the clasper and membranous dorsal lobe blunt rather than sharp and pointed. In addition the ventral spur of the



FIGS. 17-23.—Male genitalia of *Electragapetus* (*E.*) and *Agapetus* (*A.*): A, Lateral aspect; B, dorsal aspect; C, ventral aspect of clasper. (aed, aedeagus; c, cercus; cl, clasper; l, left lobe; r, right lobe.)

clasper is short in *membrosus*, long and pointed in the *bidens* group.

*Male*.—Length 3 mm. Color dark brown, nearly black, the venter and legs slightly lighter. General structure typical for genus. Hind wing, Fig. 12, with Sc close to but slightly separated from margin;  $R_{2+3}$  with minute branch at extreme apex; anal veins with base of 2A and apex of 1A forming a straight serial vein, beneath which is a single loop of doubtful composition (see discussion above for *membrosus* group). Fifth sternite with lateral areas embossed. Genitalia as in Fig. 18. Tenth tergite divided into a pair of stout, curved arms. Cercus represented by a thin strap embedded in membrane, the end of the strap with a single long seta. Clasper with a short, triangular main piece with a dorsal membranous lobe and a ventral truncate projection. Aedeagus with simple rods.

*Female*.—Length 3.5 mm. Color and general structure as in male. Middle legs with tibia and basitarsus expanded, foliaceous, and concave mesad. Abdomen slender and pointed.

*Holotype*.—Male; Unlong-kong (above), Szechwan, China, 12,000–15,000 feet elevation, July 3, 1929, H. Stevens.

*Allotype*.—Female; Tu-pa-keo, Szechwan, China, 7,400 feet elevation, September 3, 1929, H. Stevens.

*Paratypes*.—All from Szechwan, China, H. Stevens: same data as for holotype, 2♂; same data as for allotype, 1♀; same as for allotype, but September 5, 2♂; between Shuang-yo and Tu-pa-keo, August 30, 1929, 1♂. Holotype, allotype, and three paratypes in the Chicago Natural History Museum; three paratypes in the collection of the Illinois Natural History Survey.

***Agapetus denningi*, n. sp.**

The genitalia indicate that this species belongs to the small complex including *ophionis* Ross and *taho* Ross and is an especially close relative of *taho*. From this species, *denningi* differs in having a more triangular lateral aspect of the clasper and an almost even dorsal outline of the tenth tergite, which ends in a simple, downcurved point. It is likely that *denningi* represents a condition close to that of the ancestor of the complex.

*Male*.—Length 5 mm. Color dark brown, slightly lighter on legs and venter. General structure typical for genus, and for subgenus as described above. Genitalia as in Fig. 23. Ninth segment nearly annular, with anterior margin evenly bowed. Tenth tergite with lobes bladelike and thin, each with lateral aspect fairly shallow, triangular, elongate, and ending in a sclerotized portion which is curved ventrad and beaklike. Cercus moderately long and slender, with an irregular row of long setae. Clasper with base massive, apex tapering to a point curved sharply mesad; at the dorsal apex of the basal portion is a short, sharp projection pointed mesad. Aedeagus with simple rods.

*Female*.—Size, color, and general structure as for male. Female characters typical for *ophionis* complex, for which means of specific separation in this sex are not yet known.

*Types*.—Holotype, male, Rouge River National Forest, Oreg. Allotype, female, and paratype, male, same data. Holotype and allotype in the collection of D. G. Denning, paratype in the collection of the Illinois Natural History Survey.

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